

Ecology of the sea hare *Aplysia parvula* (Opisthobranchia) in New South Wales, Australia

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Abstract

The present study investigates the host range, distribution, abundance, activity and feeding preferences of the sea hare *Aplysia parvula* on the New South Wales (NSW) central and south coast. *Aplysia parvula* was found to occur mainly on red algae, especially *Delisea pulchra* and *Laurencia obtusa* near Sydney, NSW. The abundance of *A. parvula* was positively related to the abundance of *D. pulchra* and *L. obtusa* and sea hares were absent when survey sites lacked these algae. *Aplysia parvula* occurred in greater abundance on *L. obtusa* compared with *D. pulchra*, although *L. obtusa* is ephemeral near Sydney. Fluctuations in the abundance of *A. parvula* on *D. pulchra* suggest that *A. parvula* individuals persist for only a few months and are short lived. *Aplysia parvula* appears to prefer small *D. pulchra* plants with lower levels of secondary metabolites. The diet of *A. parvula* was not restricted to host algae, because animals consumed a range of co-occurring red, green and brown seaweeds. *Aplysia parvula* was nocturnally active on host algae; it grazes and copulates in the canopy of host algae at night, as well as moving between plants. *Aplysia parvula* may compete with other herbivores (notably *Aplysia dactylomela*) for the less-abundant *L. obtusa* resource. Interspecific competition appears less likely on *D. pulchra*, because few other sea hares were found on this seaweed.

Additional keywords: abundance, algal diet, consumption, diel activity, habitat choice, herbivore.

Introduction

A considerable body of literature exists on the neurophysiology and anatomy of sea hares. In comparison, relatively little is known of the natural history and ecology of these molluscs. Some studies have investigated the population ecology of sea hares (Sarver 1979; Gev *et al.* 1984; Pennings 1991a), whereas others have considered their activity patterns (Carefoot and Taylor 1988; Carefoot 1989, 1991; Pennings 1991b). The natural products of sea hares have been studied extensively (for a review, see Avila 1995), yet the ecological role of acquired secondary metabolites is still debated (e.g. Pennings and Paul 1993; Rogers *et al.* 2002).

Many authors have noted spatial and temporal variation in the abundance of sea hares (for a review, see Carefoot 1987) and sea hares are generally considered to be ephemeral in occurrence. Adult abundance is generally less than a few individuals per square metre, except for breeding aggregations (Carefoot 1987). Factors that influence the abundance of sea hares include physical processes that affect larval supply, survival of recruits and habitat suitability (Sarver 1979; Carefoot 1987; Pennings 1991a), the abundance of host algae as recruitment sites and food (Sarver 1979; Gev *et al.* 1984; Pennings 1991a) and biotic interactions, including predation and competition (Sarver 1979; Achituv and Susswein 1985; Pennings 1990a, 1990b; Pennings *et al.* 2001).

Dispersal of planktonic larvae is thought to be the primary determinant of the distribution of sea hares (Sarver 1979; Pennings 1991a). Larval supply depends on the fecundity of source populations, biotic conditions affecting larval survival and physical oceanographic processes (Morgan 1995; Pechenik 1999). Sea hares with cosmopolitan distributions, such as *Aplysia parvula* (Guilding in Mörch, 1863), *A. juliana* (Quoy and Gaimard, 1832) and *A. dactylomela* (Rang, 1828) (Carefoot 1987), have resilient veliger larvae capable of prolonged existence in the plankton and widespread dispersal (e.g. Kempf 1981). Adverse physical conditions, including temperature, salinity, wave action, tidal cycles and ultraviolet radiation, can cause mortality in populations of both larval and benthic sea hares (Sarver 1979; Carefoot 1987).

Host algae (juvenile foods) are preferred sites of metamorphosis for larvae in most species of sea hare studied (Switzer-Dunlap 1978), although Pawlik (1989) found that recruitment was not limited to host algae in *A. californica* (Cooper, 1863). However, metamorphosis of *A. californica* veligers is highest on the host algae *Plocamium cartilagineum* (Linnaeus) Dixon, 1967 and *Laurencia pacifica* (Kyllin) and juvenile *A. californica* preferentially inhabit and grow best on these red seaweeds (Pennings 1990c). The abundance of *A. californica* was significantly linked to the abundance of *P. cartilagineum* within a site, but not between sites (Pennings 1990c, 1991a). Pennings (1991a) attributed differences in the abundance of *A. californica* between sites to physical oceanographic processes affecting larval supply. *Aplysia parvula* is most often found on red seaweeds and has been reported to occur on *Acanthophora spicifera* (Vahl) Borgesen, *Asparagopsis taxiformis* (Delile) Trevisan, 1845, *Laurencia* spp. (Lamouroux, 1813), *Plocamium costatum* (C. Agardh, 1822) and *Portieria* (*Chondrococcus*) *hornemannii* (Lyngbye) Silva, 1987 (Morton and Miller 1968; Willan 1979; Switzer-Dunlap and Hadfield 1981; Carefoot 1989; Faulkner 1992). In the Sydney region, *Aplysia parvula* has been found on *Delisea pulchra* (Greville) Montagne, 1844 and *Laurencia obtusa* (Hudson) Lamouroux, 1813, which occur in different habitats, as well as on *L. rigida* (J. Agardh, 1876) and the green alga *Ulva* sp. (Linnaeus, 1753) (Rogers *et al.* 1995).

The abundance of sea hares is also affected by biotic interactions. Juvenile sea hares can be subject to high rates of predation that may significantly reduce their abundance (Pennings 1990a; Rogers *et al.* 2000, 2002; Ginsburg and Paul 2001; Pennings *et al.* 2001). In contrast, adult sea hares are thought to be free from most predators (Carefoot 1987; Pennings 1990c), although adult *A. parvula* are consumed by fishes (Rogers *et al.* 2002). Competition has rarely been investigated for sea hares. One study reported the possibility of niche separation between sympatric species (Achituv and Susswein 1985), whereas another suggested competition for *Laurencia* sp. between *A. parvula* and *A. dactylomela* (Willan 1979). Carefoot (1989) argued that food was not limiting in a separate study of *A. parvula* and *A. dactylomela*.

Early neurological studies of the aplysiid eye reported a circadian rhythm (Kandel 1979) and subsequent field studies of activity patterns in sea hares by Carefoot (1985, 1989, 1991) found distinct patterns of behaviour during the diel cycle. *Aplysia dactylomela* is nocturnal, becoming active at dusk and moving to find mates, copulating, then feeding during the early hours of the morning and resting during daylight hours (Carefoot 1985). This behaviour pattern was found to be consistent between populations of *A. dactylomela* in Hawaii and Jamaica (Carefoot 1989, 1991). The activity patterns of *A. fasciata* (Poiret), *A. parvula* and *A. californica* have also been studied. All three species are active during the day and at night (Susswein *et al.* 1983; Carefoot 1989; Pennings 1991b). These studies of sea hare activity mostly considered reproductive adult populations, although the *A. parvula* individuals

investigated by Carefoot (1989) were small (<1 g live weight). The activity patterns of juvenile sea hares may vary from those of adults because of the threat of predation.

Many opisthobranchs are specialised feeders, consuming only a few types of food (Karuso 1987; Faulkner 1992; Jensen 1997). However, most adult sea hares are an exception to this general pattern, foraging on a variety of red, brown and green algae, sea grasses and cyanobacteria, although *A. juliana* consumes Ulvales almost exclusively (Carefoot 1987; Gerwick and Whatley 1989; Paul and Pennings 1991). Juvenile sea hares have restricted diets, often limited to one or a few types of algae (Pennings 1990c). Sea hares generally consume macrophytes with soft tissues that they can bite easily and avoid toughened or calcified species (Carefoot 1987; Pennings and Paul 1992). Because specimens of *A. parvula* are small even as adults (typically <5 g wet weight (wt)), they use algae as both food and habitat during their benthic life (e.g. mesogazers; Brawley 1992; Paul *et al.* 2001), unlike other larger species that forage in the open. The objective of the present study was to describe the benthic phase of the life cycle of *A. parvula* in New South Wales (NSW), its host plants, abundance, activity patterns and dietary range.

Materials and methods

Study sites and determination of host algae

The main sites for field work were Astrolabe Cove, Congwong Bay, Bare Island and Cruwee Cove on the northern shores of Botany Bay and Shark Bay and Parsley Bay in Port Jackson, near Sydney (NSW, Australia). Surveys to determine which algae *Aplysia parvula* inhabit were conducted at these sites and those listed below using SCUBA. *Aplysia parvula* is most commonly reported on red algae, so all red macroalgae encountered during dives were searched for sea hares. When sea hares were located on an alga, part of the seaweed was collected for identification. Sites from Port Jackson (33°50'S, 151°15'E) south to Narooma (36°10'S, 150°5'E) were investigated for sea hares and red algae. Localities that were studied include: Hermit Point, Blackburn Cove, Mrs Macquarie's Point, Bradleys Head, Taylor's Bay, Chowder Head, George's Head, Sow and Pigs Reef and Vaucluse Bay, all of which are in Port Jackson; Kurnell and Silver Beach on the southern shores of Botany Bay; Shelly Point, Bass and Flinder's Point at Port Hacking; Kiama; Hyam's Beach and Murray's Beach in Jervis Bay; Summercloud Bay; Kioloa; and Josh's Beach and South Brou Beach near Narooma.

Field surveys of Aplysia parvula and host algae

The distribution and abundance of *Aplysia parvula* and algae were studied at three sites (Congwong Bay, Cruwee Cove and Shark Bay) from April 1995 to July 1997. These sites were chosen based on the presence of the host algae *Delisea pulchra* or *Laurencia obtusa*, within the mixed algal communities at each site. The sites were located on sandstone reefs and varied in depth from 1 to 3 m below spring low water. Each survey area consisted of a 100-m² patch bordered by markers spaced at 10 m on the north side and on the east or west sides. Surveys were conducted on SCUBA using a grid system to randomly locate quadrats for measuring algal cover or transects to measure sea hare abundance. Quadrats consisted of a square steel frame covered with mesh (10 × 10 grid) to measure percentage algal cover using the point intercept method. For each sampling event, 10 replicate 0.25-m² quadrats were measured. Replication and quadrat size (0.25 m²) were chosen to determine patterns of algal abundance at each site within the time constraints imposed by diving. Transects were used to determine sea hare abundance because these molluscs occurred at low abundance and were widely scattered among the seaweeds. Five replicate 4 × 0.5-m (2-m²) transects were sampled by searching the substrata and all seaweeds for sea hares. Bottom water temperature (in °C) was recorded at each site during surveys using a digital depth gauge (Scubapro-Uwatec, Sydney, Australia). Surveys were conducted at 2-monthly intervals when possible. Because *A. parvula* is cryptic on host algae, search efficiency was evaluated in three replicate transects in a *D. pulchra* patch at Cruwee Cove on 25 October 1994. All *A. parvula* individuals were counted using transects as described above, then the *D. pulchra* plants were collected from each transect, taken to the laboratory and examined for sea hares. The number of sea hares counted in the field was then divided by the number found on algae in the laboratory to obtain a value for search efficiency. The mean (± s.e.m.) number of sea hares found during field transects

was $64.9 \pm 19.1\%$; hence, search efficiency was high, but juvenile sea hares were often overlooked because they are small and highly cryptic.

Collections of *D. pulchra* and *L. obtusa* were also made during the present study to measure sea hare abundance at Bare Island and Shark Bay. All collections of algae were performed haphazardly in algal patches of generally less than 50 m². Algae were placed into individual plastic bags *in situ*, then taken to the laboratory to measure sea hare abundance and the wet weight of algae. No collections of algae or sea hares were made within or near fixed survey sites.

Assessment of factors that correlate with sea hare abundance on Delisea pulchra

To investigate various factors that may influence the abundance of *Aplysia parvula* (i.e. abundance of other herbivores, plant physical characteristics or levels of secondary metabolites), collections of *Delisea pulchra* and associated epifauna were taken at Astrolabe Cove on 5 and 13 July 1995 in two areas approximately 100 m apart. The close proximity of sample areas minimised the possibility of effects resulting from differences in physical conditions. Plants were collected haphazardly from patches in each area, which were on sandstone reefs at 2–3 m depth and differed in their abundance of *A. parvula* (they appeared absent at one area), but were otherwise similar in most respects. Most of the *D. pulchra* collected had some epibionts, including encrusting coralline algae, *Ulva* sp., *Enteromorpha* sp., *Colpomenia* sp., filamentous red or brown algae and sponges. The apices of the *D. pulchra* collected were not bleached (bleaching of apices occurs during summer; C. N. Rogers, unpublished observation). Thirty plants were collected haphazardly from the algal beds (approximately 50 m² in size) in each area and placed in individual plastic bags with 2–3 L sea water. In the laboratory, each plant was searched and the numbers of *A. parvula*, the gastropods *Phasianotrochus eximius* (Perry, 1811) and *Dentimitrella lincolnensis* (Reeve, 1859) and the sea urchin *Holopneustes purpureescens* (Agassiz, 1872) were recorded. These species were the most abundant herbivores found on *D. pulchra*. Other epifauna included decorator crabs (*Naxia* sp.), Ophiuroidea, dorid and aeolid nudibranchs and errant and sedentary polychaete worms; data for these less abundant epifauna are not presented here. Physical data for each plant were also recorded, including wet weight (wt), length from holdfast to apices and breadth at canopy, then each plant was frozen for chemical analysis. Whole *D. pulchra* plants were freeze-dried, ground to powder and 200 mg was then extracted using 5 × 5 mL aliquots of 100% analytical grade dichloromethane. Samples were quantitatively analysed for secondary metabolites using gas chromatography–mass spectrometry following the methods of de Nys *et al.* (1996). Two additional measures of the physical characteristics of *D. pulchra* plants were also calculated. The first was emersed plant volume, which was calculated using the formula for the volume of a cone (because *D. pulchra* often has a conical habit at shallow depths). The second was plant density, which was calculated by dividing plant wet wt by volume. This measure gives an indication of the packing of algal thalli, bulky plants having more thalli per unit volume (higher density) compared to plants with sparse thalli.

Activity patterns of Aplysia parvula

The activity patterns of *Aplysia parvula* were recorded *in situ* using SCUBA to observe sea hares on 15 tagged *Delisea pulchra* plants. Tags were relocated if sea hares moved from marked plants. The activity of sea hares was classified into four categories, which are (in order of decreasing energetic requirement) as follows: moving, grazing, copulating and resting (Carefoot 1989). Where sea hares were engaged in more than one activity (e.g. grazing and copulating), these were recorded, although only the most energetic activity is presented for each individual (i.e. one individual as grazing and the second sea hare as copulating). Dives to record activity were staggered over consecutive weeks, each being separated by at least 12 h because activity may not be independent during shorter periods (Pennings 1991b). Activity was observed for eight different time periods during November 1998. The activity patterns of *A. parvula* on *Laurencia obtusa* were observed during a separate study of sea hare movements (Rogers *et al.* 1998). Observations at night were made using torches to illuminate plants and typically lasted less than 1 min. *Aplysia parvula* often moves between algae after being illuminated at night (Rogers 1999); however, this behaviour did not affect determination of activity patterns because this movement occurred after observations were made. When animals were not visible on tagged plants, thalli were parted and searched to locate sea hares.

Dietary range of Aplysia parvula

The dietary range of *Aplysia parvula* was assessed in a no-choice consumption experiment that included the host plant *Delisea pulchra* and co-occurring red, green and brown algae. Individual *A. parvula* were weighed (mean size 0.554 ± 0.019 g wet wt) and then placed into separate cells of 25-L experimental

aquaria (divided into 20 cells per aquarium) supplied with flowing seawater. Five replicate sea hares were offered each seaweed species and three additional replicate pieces of each seaweed (autogenic controls) were placed in cells without sea hares to measure changes in mass unrelated to consumption. Algae were assigned randomly to cells across treatments.

The red seaweeds used were *Amphiroa anceps* ((Lamarck) Decaisne, 1842), *Gracilaria halogenea* (Millar, 1990), *Galaxaura marginata* ((Ellis & Solander) Lamouroux, 1816), *Asparagopsis armata* (Harvey, 1855), *Nitophyllum delicatum* (Millar, 1990), *Laurencia rigida*, *Scinaia australis* ((Setchell) Huisman, 1985), *Solieria robusta* ((Greville) Kylin, 1932), *Hypnea johnstonii* (Setchell & Gardner, 1924) and the apical parts of bleached and healthy *D. pulchra*. *Delisea pulchra* at shallow depths (<5 m) becomes bleached on the apical parts of the thalli during spring/summer and may be less palatable to *A. parvula*. The green seaweeds used were *Caulerpa scapelliformis* ((R. Brown ex Turner) C. Agardh, Harvey, 1858) and *Ulva* sp. The brown seaweeds used were juvenile *Ecklonia radiata* (Hornemann, 1828), *Sargassum vestitum* ((R. Brown ex Turner) C. Agardh, 1820), *Sargassum linearifolium* ((Turner) C. Agardh, 1820), *Colpomenia sinuosa* ((Mertens ex Roth) Derbes and Solier, 1851), *Dictyota dichotoma* ((Hudson) Lamouroux, Harvey, 1847) and *Zonaria diesingiana* (J. Agardh, 1841).

Seaweeds were identified using existing keys (Womersley 1984, 1987; Farrant and King 1988; Millar 1990) and were collected on 12 November 1997 from Astrolabe Cove, Congwong Bay or Shark Bay. The pieces of seaweed used were 0.5–1 g (wet wt) and sea hares were allowed to feed for 3 days, after which time each piece was reweighed. Pieces were taken from the upper parts of large seaweeds, whereas whole plants were used for smaller species. Consumption data are presented as g wet wt seaweed eaten per g wet wt *A. parvula* per day ($\text{g g}^{-1} \text{day}^{-1}$) so as to correct for differences in the size of sea hares. Before calculation of these values, data for each seaweed were corrected for autogenic changes by subtraction of the mean change in the mass of autogenic controls.

Statistical analyses

Abundance data for *Delisea pulchra*, *Laurencia obtusa* and *Aplysia parvula* at survey sites were highly heteroscedastic following appropriate transformations and Cochran's test, so no formal comparison was made between survey sites. To investigate whether there was a relationship between the abundance of *A. parvula* and that of *D. pulchra*, data from the Cruwee Cove and Congwong Bay survey sites (where both *A. parvula* and *D. pulchra* occurred) were pooled, then analysed by linear regression. To determine whether there was a relationship between the abundance of *A. parvula* and sea temperature, survey data for Cruwee Cove and Congwong Bay were pooled and analysed by linear regression.

Collections of *D. pulchra* from Astrolabe Cove (July 1995) were combined and analysed as one data set using linear regression to determine whether there was any relationship between the abundance of sea hares and the variables measured (abundance of other herbivores, algal physical characteristics or levels of secondary metabolites). The abundance of *A. parvula* on *D. pulchra* or *L. obtusa* in collections (no. g^{-1} algae) was also compared using Student's *t*-test. The frequency of activity of *A. parvula* on *D. pulchra* was analysed using a *G*-test with Williams's correction (Sokal and Rohlf 1995) to test the null hypothesis that activity is independent of diel sampling time. The mean consumption of different seaweeds by *A. parvula* was compared with zero by Student's *t*-test using Excel 4.0 (Microsoft Corp., Seattle, WA).

Results

Distribution of *Aplysia parvula*

Aplysia parvula was found on four species of algae during surveys at Congwong Bay, Cruwee Cove and Shark Bay. Of the 206 animals found during surveys, 82.5% occurred on *Delisea pulchra*, 13.1% occurred on *Laurencia obtusa*, 3.9% occurred on *Sargassum linearifolium*, and 0.5% occurred on *Dictyota dichotoma*. At other sites investigated on the NSW south coast, *A. parvula* was observed on several red algae, including *Asparagopsis armata*, *Plocamium cartilagineum*, *Solieria robusta* and an unidentified *Laurencia* sp. These red algae were uncommon or ephemeral in occurrence and non-coralline rhodophytes generally represented a small proportion of algal cover at survey sites (Fig. 1), except at Congwong Bay, where *Delisea pulchra* formed dense patches.

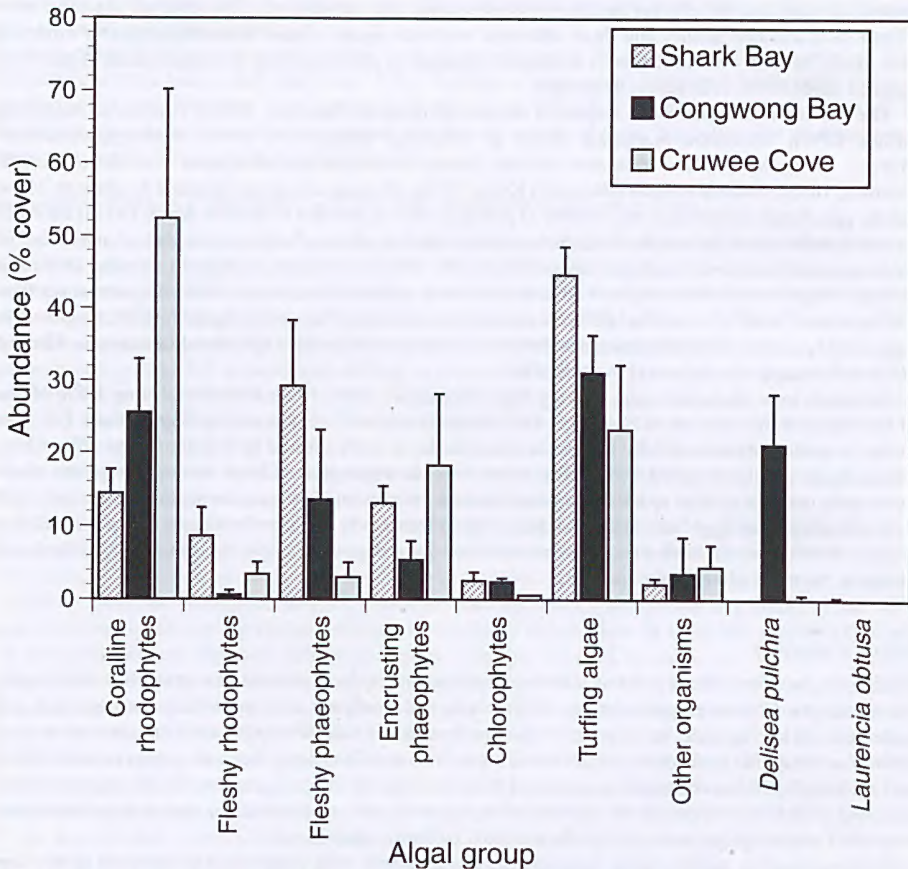


Fig. 1. Mean ($\pm$ s.e.m.) abundance (percentage cover) of algal groups and the host algae (*Delisea pulchra* and *Laurencia obtusa*) of *Aplysia parvula* at field sites for all surveys.

Abundance of Aplysia parvula and host algae

Delisea pulchra occurred in high abundance at the Congwong Bay site (mean ($\pm$ s.e.m.) $21.5 \pm 7.0\%$ cover), although this population declined in abundance over time (Fig. 2a). Coincident with the final phase of this decline was the mass recruitment of the sea urchin *Heliocidaris erythrogramma* (Valenciennes, 1846) onto the reef at Congwong Bay (see Wright and Steinberg 2001). The abundance of *Delisea pulchra* was consistently low at Cruwee Cove ($0.4 \pm 0.2\%$ cover), as was that of *Laurencia obtusa* at Shark Bay ($0.2 \pm 0.1\%$ cover; Fig. 2b,c). *Laurencia obtusa* did not reach the high abundances observed prior to surveys at Shark Bay; it is seasonal in occurrence (Fig. 2c), but can form dense patches during the summer or autumn in Port Jackson. *Aplysia parvula* was found infrequently on the brown seaweed *Sargassum linearifolium*. Brown seaweeds (especially the genus *Sargassum*) were abundant at survey sites, except Cruwee Cove (Fig. 1). Coralline red algae also formed a substantial proportion of algal cover across survey sites and turfing algae (typically filamentous forms <3 cm) were also abundant at all sites (Fig. 1).

Aplysia parvula was most abundant at Congwong Bay (Fig. 2a), with generally lower abundance at Cruwee Cove and Shark Bay (Fig. 2b,c), although the highest abundance of

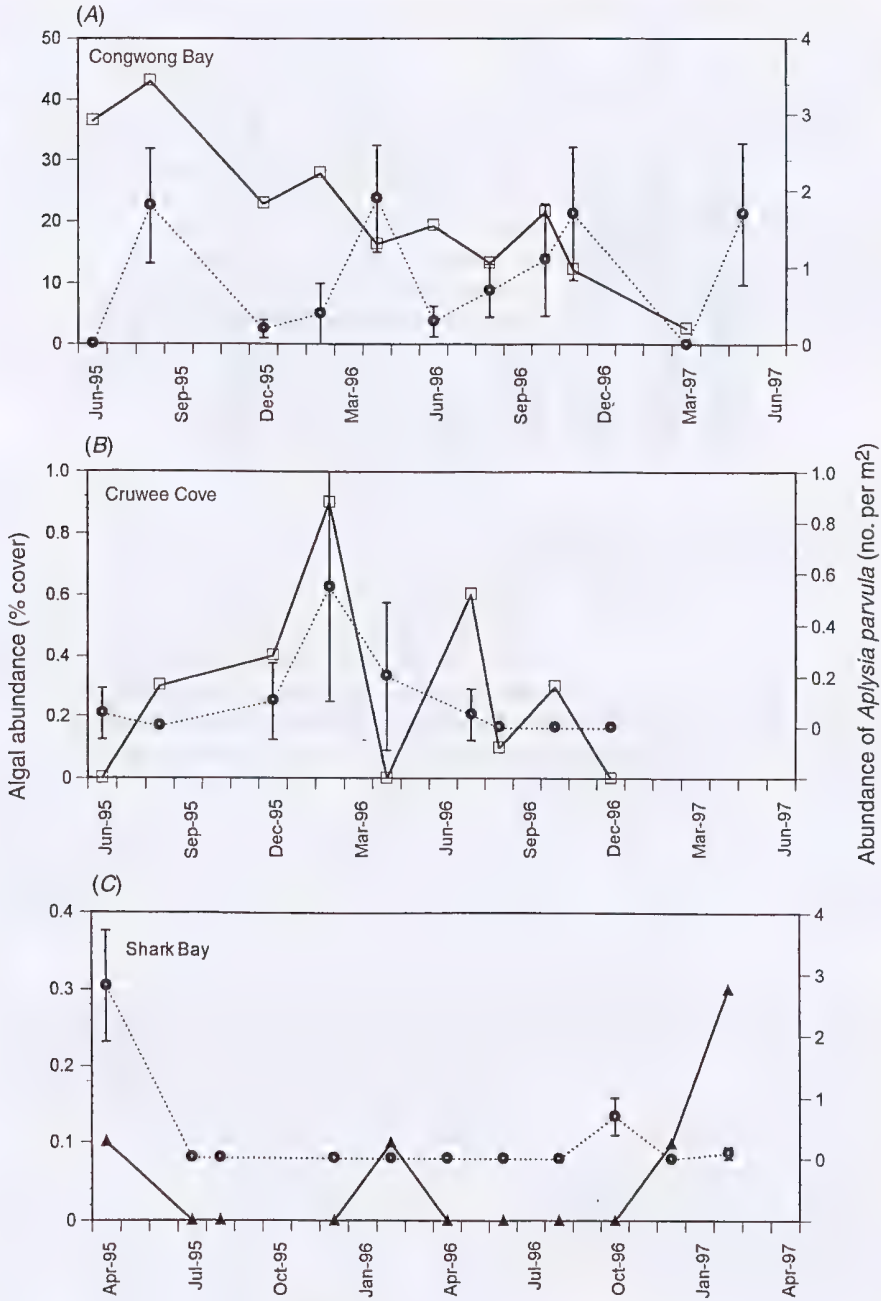


Fig. 2. Abundance of *Aplysia parvula* and host algae at fixed sites during temporal surveys. The mean ($\pm$ s.e.m.) abundance of *A. parvula* (●) is shown for each survey. A, Congwong Bay surveys, including the mean abundance of *Delisea pulchra* (□). B, Cruwee Cove surveys, including the mean abundance of *D. pulchra* (□). C, Shark Bay surveys, including the mean abundance of *Laurencia obtusa* (▲). Error bars for algal abundance were omitted to emphasise variation in sea hare abundance.

A. parvula recorded during surveys was 2.80 ± 0.92 sea hares per m^2 on *L. obtusa* at Shark Bay. *Aplysia parvula* was present year round on *D. pulchra* and was present during the summer and autumn on *L. obtusa* (Fig. 2). *Aplysia parvula* inhabiting *D. pulchra* at Congwong Bay appeared to show regular peaks in abundance separated by intervals of 6–8 months (Fig. 2a) that were of similar magnitude, despite the declining abundance of *D. pulchra*. There was a significant relationship between the abundance of *A. parvula* and percentage cover of *D. pulchra* ($y = 0.25x + 0.06$; $r^2 = 0.32$; $P = 0.01$; $n = 18$) for pooled data (Cruwee Cove and Congwong Bay). The low abundance of *L. obtusa* at the Shark Bay site precluded an analysis of the relationship between the abundance of *A. parvula* and this seaweed. The abundance of *A. parvula* on *D. pulchra* (pooled data) showed no relationship to sea temperature when examined using linear regression ($y = -0.03x + 1.41$; $r^2 = 0.01$; $P = 0.720$, $n = 18$). Overall, *D. pulchra* occurred in greater abundance than *L. obtusa* in both space and time, and *D. pulchra* was the major host plant for *A. parvula* near Sydney.

Factors associated with variation in the abundance of Aplysia parvula

Delisea pulchra was collected to investigate biotic, physical and chemical factors that may influence the abundance of *Aplysia parvula* on this seaweed. There were significant relationships between the abundance of *A. parvula* and several of the variables measured (Table 1). The only positive relationship found was between the abundance of *A. parvula* and that of the herbivorous 'prosobranch' gastropods recorded (see Materials and methods). Other significant linear regressions had negative slopes, including plant weight and the concentrations of the secondary metabolites (furanone 1, furanone 2 and total furanones). There was no significant relationship between sea hare abundance and the physical characteristics of plant conical volume or density. These results suggest that *A. parvula* prefer to inhabit smaller plants with lower levels of metabolites. However, the r^2 statistics for these regression analyses are low (Table 1), which diminishes their biological significance. Collections of algae showed a different pattern of abundance of sea hares compared with surveys. *Aplysia parvula* was significantly more abundant on individual *Laurencia obtusa* plants (mean 0.214 ± 0.027 sea hares g^{-1} algae wet wt; $n = 28$ plants) than on *Delisea pulchra* (0.068 ± 0.028 sea hares g^{-1} algae wet wt; $n = 15$ plants) when compared

Table 1. Factors affecting the abundance of *Aplysia parvula* on *Delisea pulchra*

Regression analyses of the abundance of *A. parvula* (no. sea hares per g wet weight (wt) algae) compared with the abundance of co-occurring herbivores (no. herbivores per g wet wt algae) or the physical and chemical properties of *D. pulchra* collected from Astrolabe Cove in July 1995. The regression equations are of the form $y = ax + b$ where y is the abundance of *A. parvula* and x is the listed variable. Significant results are indicated by asterisks ($n = 58$)

Variable	<i>a</i>	<i>b</i>	r^2	<i>P</i>
Abundance of 'prosobranch' gastropods	0.336	-0.016	0.22	<0.001*
Abundance of <i>Holopneustes purpureascens</i>	-0.450	0.017	0.02	0.419
Plant length (cm)	-0.002	0.045	0.01	0.406
Plant conical volume (cm^3)	<0.001	0.036	0.04	0.144
Plant weight (g wet wt)	-0.001	0.063	0.12	0.009*
Plant density (g cm^{-3})	0.143	0.011	<0.01	0.896
Furanone 1 concentration (mg g^{-1} dry wt)	-0.106	0.055	0.09	0.022*
Furanone 2 concentration (mg g^{-1} dry wt)	-0.071	0.041	0.08	0.038*
Furanone 3 concentration (mg g^{-1} dry wt)	-0.060	0.032	0.06	0.078
Furanone 4 concentration (mg g^{-1} dry wt)	-0.066	0.038	0.06	0.056
Total furanone concentration (mg g^{-1} dry wt)	-0.021	0.045	0.08	0.029*

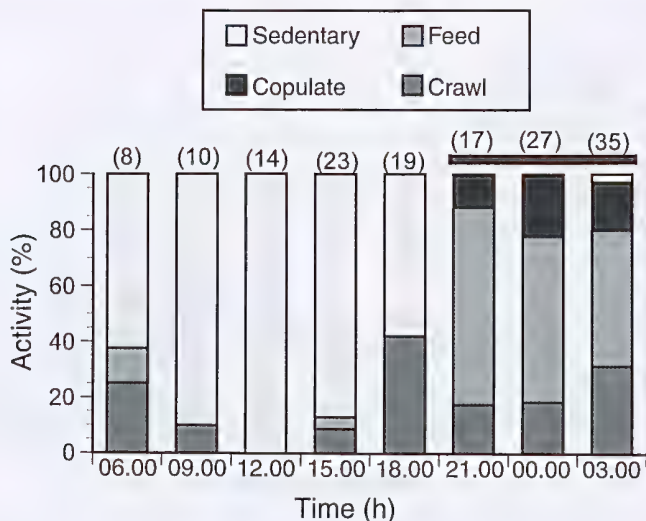


Fig. 3. Diel activity patterns of *Aplysia parvula* on *Delisea pulchra* at Congwong Bay. Histograms show the percentage of individuals engaged in each activity. The line above the bars indicates night sampling. The number of sea hares per sample (n) is given above each bar in parentheses.

using two-tailed Student's t -test ($t = -3.53$; $P = 0.001$). This difference may be attributable to the concentration of sea hares on *L. obtusa*, because this alga occurred at low abundances in Port Jackson.

Activity patterns

Aplysia parvula was nocturnal, with most sea hares grazing or copulating at night (Fig. 3). The activity of *A. parvula* on *Delisea pulchra* was not independent of diel sampling time ($G_{\text{adj}} = 151.25$, $\chi^2_{0.001[21]} = 46.80$; $P < 0.001$), suggesting that the activity of this sea hare varies significantly during the diel cycle. The population surveyed consisted of both adult and juvenile sea hares (< 1 cm in length) and all showed similar patterns of activity. *Aplysia parvula* became active during the afternoon, moving up the thalli of *D. pulchra*. After dusk, most emerged onto the canopy of *D. pulchra* and began to feed, whereas some copulated. Feeding was the most frequently recorded activity at night, although there was no apparent pattern in which activities occurred over time, with sea hares moving, feeding and mating throughout the night. Sea hares moved back down the thalli of *D. pulchra* before dawn and most remained sedentary until the following afternoon. A few *A. parvula* individuals were observed feeding on basal parts of *D. pulchra* during the day (Fig. 3). No egg laying was observed at night and egg masses were found most often in the mid to basal parts of *D. pulchra* thalli, suggesting that egg laying may occur during the day. *Aplysia parvula* had a similar pattern of nocturnal activity on *Laurencia obtusa* in Port Jackson (C. N. Rogers, unpublished observation).

Dietary range of *Aplysia parvula*

Aplysia parvula consumed a variety of co-occurring red, green and brown algae. However, red algae were consumed most often and in greater quantities than either green or brown

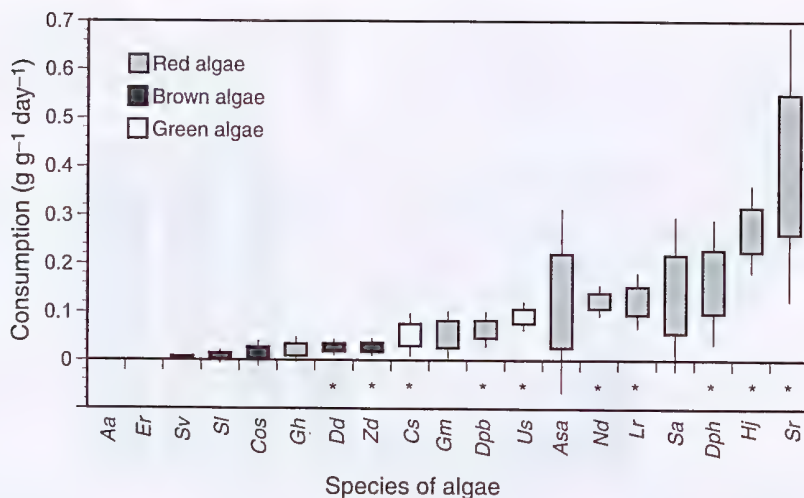


Fig. 4. Dietary range of *Aplysia parvula*. Data are the mean $\pm$ s.e.m. consumption (bars), measured as g algae eaten (wet weight) per g sea hare (wet weight) per day, and 95% confidence limits (lines). Consumption data were corrected for autogenic changes in algal mass. Mean consumption of each alga was compared with zero by Student's *t*-test. Consumption that is significantly different from zero at $P = 0.05$ is indicated (asterisk); $n = 5$ (except *Galaxaura marginata* (Gm) and *Zonaria diesingiana* (Zd), where $n = 4$). Aa, *Amphiroa anceps*; Er, juvenile *Ecklonia radiata*; Sv, *Sargassum vestitum*; Sl, *Sargassum linearifolium*; Cos, *Colpomenia sinuosa*; Gh, *Gracilaria halogenea*; Dd, *Dictyota dichotoma*; Cs, *Caulerpa scapelliformis*; Dpb, bleached *Delisea pulchra*; Us, *Ulva* sp.; Asa, *Asparagopsis armata*; Nd, *Nitophyllum delicatulum*; Lr, *Laurencia rigida*; Sa, *Scinaia australis*; Dph, healthy *D. pulchra*; Hj, *Hypnea johnstonii*; Sr, *Solieria robusta*. Algal divisions are indicated by the different shading of bars.

algae (Fig. 4). The alga *Solieria robusta* was highly consumed by *A. parvula* (at a mean rate of 0.405 ± 0.144 g g⁻¹ day⁻¹ after correction for autogenic changes). Several red algae were consumed at equivalent or higher levels than healthy *Delisea pulchra*, the host alga from which the sea hares were collected (Fig. 4). Bleached pieces of *D. pulchra* were consumed less by sea hares (0.064 ± 0.018 g g⁻¹ day⁻¹) than healthy pieces (0.161 ± 0.066 g g⁻¹ day⁻¹), suggesting that such damage lowers the palatability of the algal tissues. Consumption was significantly different from zero for eight non-host algae including red algae of the Ceramiales and Gigartinales, green algae of the Caulerpales and Ulvales, and Dicyotalean brown algae (Fig. 4). This indicates that *A. parvula* has generalised feeding habits, especially on red algae, which contrasts with their restricted distribution on host algae in the field. The brown alga *Sargassum linearifolium* was not eaten, although *A. parvula* was occasionally found on this seaweed during surveys. Consumption of the calcified red algae *Galaxaura marginata* and *Amphiroa anceps* was not significantly different from zero, yet some *A. parvula* individuals consumed the lightly calcified *G. marginata*.

Discussion

Distribution and abundance of Aplysia parvula and host algae

Aplysia parvula was found primarily on red seaweeds from three different orders (Bonnemaisoniales, Ceramiales and Gigartinales), similar to host ranges reported

previously for this sea hare (Willan 1979; Switzer-Dunlap and Hadfield 1981; Carefoot 1987, 1989). *Aplysia parvula* also occurred at very low densities on the brown algae *Sargassum linearifolium* and *Dictyota dichotoma*. Many of the red seaweeds investigated here were uncommon and/or seasonal and habitation of such seaweeds (e.g. *Laurencia* spp., *Asparagopsis armata*) by *Aplysia parvula* suggests that this sea hare is highly opportunistic, using any suitable algae. For *A. parvula*, host plant choice appears restricted to chemically rich red seaweeds that may allow this sea hare to evade and/or deter predatory fish (Ginsburg and Paul 2001; Rogers *et al.* 2002). The processes affecting the distribution of *A. parvula* (e.g. selective larval settlement, post-settlement mortality) were not tested in the present study.

Aplysia parvula was most abundant on two red algae, namely *Delisea pulchra* and *Laurencia obtusa*, near Sydney. These algae differ in occurrence; *D. pulchra* was present year round and formed large beds at some sites. *Delisea pulchra* has been reported to be one of the most abundant red seaweeds on the NSW coast (Millar 1990) and, thus, provides *A. parvula* with access to a large, persistent resource. The abundance of *A. parvula* was significantly related to the abundance of *D. pulchra*. In contrast, *L. obtusa* was found mainly in Port Jackson, where it occurred occasionally in dense patches. The relationship between the abundance of *L. obtusa* and that of *A. parvula* could not be adequately addressed from the Shark Bay survey data, because *L. obtusa* did not occur at the high abundances observed previously. However, the abundance of *A. parvula* on *L. obtusa* was measured in collections from other parts of Port Jackson and sea hares were threefold more abundant per gram *L. obtusa* compared with *D. pulchra*. *Laurencia obtusa* has been reported to be widespread in temperate and tropical waters (Millar 1990) and may provide a major resource for *A. parvula* at other localities.

Aplysia parvula occurred year round on *D. pulchra*, although its abundance on this seaweed fluctuated. Pennings (1991a) found *A. californica* to be present year round and attributed changes in its abundance to variation in recruitment. Fluctuations in the abundance of *A. parvula* may also be due to variable recruitment, although this was not measured in the present study. Another possibility is predation pressure on *A. parvula*, because some reef fish are now known to consume sea hares (Ginsburg and Paul 2001; Pennings *et al.* 2001; Rogers *et al.* 2002) and fish were observed to feed from *D. pulchra* both during the day and at night (C. N. Rogers, unpublished observations). Such continuous predation pressure may rapidly reduce sea hare populations during and after recruitment events. Although the age structure of *A. parvula* was not examined, the variable pattern of abundance suggests that *A. parvula* may persist for only a few months on *D. pulchra*.

The abundance of *A. parvula* on *D. pulchra* was weakly associated with several factors. Abundance was negatively related to the weight (size) of *D. pulchra*. One possible explanation for this pattern is that smaller plants are younger and have more palatable tissues, which are preferred by herbivores (e.g. Cronin and Hay 1996). The positive relationship between the abundance of *A. parvula* and the abundance of other herbivorous gastropods (i.e. *Phasioanotrochus eximius* and *Dentimitrella lincolnsensis*) may also indicate that smaller *D. pulchra* individuals are, in general, higher preference foods for mesograzers. The negative relationships between the abundance of *A. parvula* and concentration of secondary metabolites (furanones 1 and 2 and total furanones) may indicate that this sea hare prefers to inhabit algae with lower concentrations of these compounds. This result further supports the notion that consuming *Delisea pulchra* has a fitness cost for *A. parvula* (Rogers *et al.* 2002). No other study has attempted to relate sea hare abundance on host plants to their physical and chemical properties, so it is unknown

how general these results are. The red algae inhabited by *A. parvula* typically have complex habits, with densely packed thalli. However, *A. parvula* showed no preference for high thalli density among *D. pulchra* individuals. Other marine herbivores, including amphipods (Hacker and Steneck 1990) and crabs (Kennish and Williams 1997), show strong preference for seaweeds with particular morphologies. Suggested reasons for such selectivity include refuge value, attachment ability and restricted feeding structures (Hacker and Steneck 1990; Kennish and Williams 1997).

Activity patterns

Aplysia parvula was mostly active at night on *Delisea pulchra* and *Laurencia obtusa* near Sydney, moving, grazing and copulating in the canopy of these algae. In contrast, *A. parvula* in Hawaii is active over the entire diel cycle, with grazing occurring mostly in the afternoon (Carefoot 1989). Furthermore, Hawaiian *A. parvula* occupies cryptic positions at the base of algae at night rather than during the day (Carefoot 1989). The sea hare *A. dactylomela* exhibits the same nocturnal activity patterns in Hawaii (Carefoot 1989) and Jamaica (Carefoot 1991), and *A. dactylomela* in Port Jackson was also observed to be nocturnal, although large adults change their habits and forage or copulate during the day. The factors affecting activity patterns in sea hares appear to vary with ontogeny (at least for *A. dactylomela*) and geographic location and may warrant further research.

Diet and feeding by Aplysia parvula

Aplysia parvula consumed a variety of red, green and brown algae. This generalised feeding pattern is similar to that found for other sea hares (Carefoot 1987). However, this contrasts with the restricted distribution of *A. parvula* on *Delisea pulchra* and *Laurencia obtusa* that was found during field surveys. *Solieria robusta* (which lacks known secondary metabolites) was eaten at the highest rate by *A. parvula*, but is uncommon and grows in deeper habitats than those in which *A. parvula* is typically found. The sparsely branched habit of *S. robusta* may provide less shelter from predators for sea hares compared with other host algae. Interestingly, several red seaweeds were consumed at higher rates than the dominant host *D. pulchra* from which the *A. parvula* individuals were collected. The host alga *L. obtusa* (not tested here) was consumed at the greatest rate by *A. parvula* in the study of Rogers (1999), with a mean ($\pm$ s.e.m.) feeding rate of 0.884 ± 0.043 g g⁻¹ day⁻¹, some fivefold greater than for *D. pulchra*. *Aplysia parvula* preferentially consumed the apical tissues and lateral buds of both *D. pulchra* and *L. obtusa* (Rogers 1999). Such preferences for softer or younger tissues have been reported previously in sea hares (Carefoot 1987; Pennings 1990a) and other marine herbivores (Poore 1994; Cronin and Hay 1996). *Aplysia dactylomela* and *A. sydneyensis* (Sowerby, 1869) also consume *L. obtusa* and inhabit it as juveniles (C. N. Rogers, unpublished observation). Juveniles of these species may compete with *A. parvula* for *L. obtusa*, as suggested by Willan (1979). *Aplysia parvula* has more exclusive use of *D. pulchra* because only a few individual *A. juliana* and *A. sydneyensis* were found on this alga during surveys.

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